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ORIGINAL ARTICLE

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Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada

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Abstract Little is known about the responses of large, old trees to release from competition, though such trees are of great interest in forest ecology, conservation and silviculture. Increment cores were taken from mature eastern white pines (*Pinus strobus* L.) in 144 sample points in 12 partially harvested and 6 unharvested control stands in Ontario, Canada, to determine how these trees responded to a 'structural retention harvest' that had occurred 9 years previously. Prior to harvest, increment growth was slightly lower in control stands, but not significantly so. Strong correlation in diameter increments among stands indicates external climatic forcing or internal synchronicity, e.g. reproductive allocation. Three years after harvest, growth in harvested stands overtook that in control stands, and increased to 63±8% SE above expected levels by 8 years after harvest. The study demonstrates the ability of old trees to respond markedly to reduced competition, questioning the concept of an age-related decline in forest productivity. In addition to increased timber production, growth responses of old trees have important implications for stand regeneration, wind firmness, and maintenance of wildlife habitat elements following partial stand harvests. Comparison of disturbed stands with undisturbed stands allows better estimation of tree responses than methods in which disturbance is inferred from diameter increment variation within individual trees.

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Introduction

Thinning to stimulate growth of remaining trees is a common silvicultural practice (Smith et al. 1997), the earliest examples of which date back to the fourteenth century Prussia (Brandl 1992). Prescribed thinning usually takes place early in stand development, allowing foresters to pre-empt natural competition-related mortality and to select desirable trees for continued growth. Stocking density, competition, and mortality rates are greatest early in stand development in both natural and managed stands (Oliver and Larsen 1996; Weller 1987), and young trees are generally thought to show the largest growth responses to reduced competition (discussed in Nowacki and Abrams 1997). Consequently, most studies have focused on growth responses of small, young trees to thinning. In contrast, the influence of competition on old, 'decadent' trees has largely been ignored, since growth rate declines with tree age (Ryan et al. 1997) and old trees are often harvested before quality declines or death occurs.

Recently, however, interest in the biology of large old trees has increased (Bond and Franklin 2002), driven by recognition of the importance of 'old-growth' forests for biodiversity and ecosystem function (Lindenmayer and McCarthy 2002; Marcot 1997; Naylor 1994) and the realization that such forests are becoming rare following centuries of intensive clearance. Such concerns have led to modified silvicultural systems in several jurisdictions to minimize negative impacts on the forest ecosystem. For example, *structural retention harvests* (Franklin et al. 1997) leave a greater proportion of live trees, snags, coarse woody debris (cwd) and other legacies of the original stand that are important resources to the forest biota.

Eastern white pine (*Pinus strobus* L.) is an example of an economically and ecologically important tree species that has been massively exploited (Aird 1985), and conserving and managing the remaining white pine forests

is now the subject of much debate (Clark and Perera 1995; Earthroots 2002; Old-Growth Policy Advisory Committee 1994). Most research on white pine growth and competition has been conducted on trees less than half the maximum age of this species, which may exceed 300 years (Abrams and Orwig 1996). Annual volume increment reaches a maximum at 60–80 years in natural stands and at ~25 years in plantations (Burns and Honkala 1990). Stand basal area increases rapidly until ~60 years, after which it levels off or increases slightly as it is balanced by mortality (Horton and Bedell 1960, p 113). White pine is moderately shade tolerant and requires release from canopy competition as a sapling (Stiell 1985). Stiell (1979) found that reducing density in a 19-year-old plantation by removing dominant trees disfigured by white pine weevil (*Pissodes strobi* Peck) doubled diameter increment over the following decade. An 80% increase in volume increment was found 20 years after removing the hardwood overstorey in 55-year-old white pine (Stiell et al. 1994). Shelterwood cuts are commonly applied to white pine, both to reduce the incidence of weevil attack on regeneration (Wallace and Sullivan 1985) and to increase volume growth and seed production of residual overstorey trees (Smith et al. 1997). However, little is known about how the remaining mature trees respond to such partial cutting.

In this study, increment cores were used to investigate the response of large, old white pines to a structural retention harvest. The null hypothesis that diameter increment in mature white pines is not influenced by partial stand harvest was tested by comparing diameter increments of trees in partially harvested stands with those in unharvested control stands.

Materials and methods

Study site

The study was conducted in the vicinity of Galloway Lake in the Algoma Region of central Ontario, 83°55′W, 47°13′N. The topography is undulating, ranging from 450 to 600 m a.s.l., and the area contains many small lakes. Soils vary in quality and depth, ranging from moist peaty bogs on sandy depressions to thin discontinuous organic mats on rocky outcrops. The parent material is granite of the Canadian Shield. White pine stands occur mainly on fresh, very fine silty and loamy sands. The study site lies in the Boreal–Great Lakes-St. Lawrence transition zone, with variable stand composition, size and age. Boreal species found include black spruce [*Picea mariana* (Mill.) BSP], white spruce [*Picea glauca* (Moench) Voss], balsam fir [*Abies balsamea* (L.) Mill.] and white birch (*Betula papyrifera* Marsh). The Great Lakes-St. Lawrence Forest region is represented by sugar maple (*Acer saccharum* Marsh), red maple (*Acer rubrum* L.), eastern white pine (referred to as white pine from hereon), red pine (*Pinus resinosa* Ait.), eastern white cedar (*Thuja occidentalis* L.) and yellow birch (*B. alleghaniensis* Britt). White pine formed a super-canopy with a height of around 30 m, while the other species formed a lower canopy with a height of around 15 m (unpublished data).

Harvest method

Old-growth white pine stands were harvested between September and December 1992 using prescriptions designed to maintain selected old-growth forest characteristics, such as structural heterogeneity and age diversity. White pine was harvested, with residual trees a mix of healthy seed bearers and declining quality trees that would provide cavities, snags and eventually cwd. Unusable (cull) timber was left on site. As many large snags were retained as possible, with some limitations imposed by health and safety regulations.

Survey method

In August 2001, 12 harvested and 6 control stands were surveyed. Selected stands contained, or had contained prior to harvesting, a high density of large white pines. Ontario Forest Resources Inventory (FRI) maps and aerial photographs were used to help identify suitable stands. The study was conducted in stands that may be classified as old-growth, i.e. containing a high density of large, old white pines (Clark and Perera 1995) older than 120 years (Uhlig et al. 2002). Previous studies in this area have estimated white pine stand ages to be in excess of 200 years (Buchert et al. 1997; Rajora et al. 2000).

Sample points were placed within stands on a 100-m ×100-m grid using FRI stand maps. Stand area varied from 3 ha to 104 ha, with mean a 25.7 ha ±7.8 SE. The number of sample points varied with the size of the stand, giving a total of 55 sample points in control stands and 89 sample points in harvested stands. Co-ordinates of points were entered into handheld GPS units (Garmin 12XL, Garmin, Kansas, USA), allowing location of sample points in the field. Prism sweeps using a BAF 2 prism for trees, snags and stumps $\geq$10 cm diameter at breast height (dbh) were conducted at each point (Philip 1994). Species, dbh, crown class, and condition were recorded for live trees $\geq$10 cm dbh that were included in each sample. Species, diameter at 0.3 m height, and distance to stump were recorded. Horizontal distances from the sampling point to stumps, and to trees and snags that were borderline for inclusion and difficult to view through the prism, were recorded using handheld laser range finders (Forest Pro, Laser Technology, Colo., USA) to enable calculation of angle subtended, and thus whether the object was included in the sample.

At each sample point, short cores (~20 cm) were taken at breast height (1.3 m) from the nearest co-dominant, dominant, or emergent white pine that had been included in the prism sweep, from the side of the tree facing the sample point. No cores were taken from points in which no white pine had been sampled. Cores were labelled and stored in cardboard straws for analysis. In the laboratory, cores were mounted in wooden holders and sanded to clarify annual rings. Ring widths from 1960 to 2001 were measured using the TRIM (Tree Ring Increment Measurer) system developed by D.C.F. Fayle and D.C. MacIver at the Ontario Ministry of Natural Resources. Data were recorded on a personal computer running SAMSYSTEM (Stem Analysis Measurement System) software developed by R.J. Miller at the Ontario Forest Research Institute.

Analysis

The dbh of trees of which only stumps remained was calculated using a taper equation (r^2=0.97, P<0.0001), which had been determined by measuring stump diameter and dbh of 432 white pine trees in central Ontario (unpublished data). The composition of harvested stands prior to harvesting was reconstructed using these adjusted values.

Growth-ring series were checked for missing or false rings using the COFECHA program (Holmes 1983). The program fitted a cubic smoothing spline with a cut-off of 32 years to each series, and each value was divided by the corresponding value of the spline curve to remove long-

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Table 1 Description of harvested and control stands, mean ± SE. Differences between stand types were determined using *t*-tests for normally distributed data, and Mann-Whitney tests for other distributions

Variable	Control	Harvested	*P*
White pine basal area (pre-harvest), m^2 ha^{-1}	16.6±1.7	13.4±0.9	0.212
Total basal area (pre-harvest), m^2 ha^{-1}	31.6±1.6	27.3±1.1	0.009
Harvested white pine basal area[a], m^2 ha^{-1}	0.0	6.5±0.6	-
White pine dbh (pre-harvest)[a], cm	55.5±0.8	54.8±0.6	0.509

[a] Estimated from stump diameters using taper equations

term trends. Autocorrelation was removed using the autoregressive modelling function of the program. The values were then log-transformed to weigh proportional differences in measures equally. A master dating series was created from the mean of all series. Individual series were compared to the master series by correlating 20-year segments, lagged by 10 years (i.e. years 1–20, 11–30 etc.). Correlations for each segment were inspected, along with correlations for segments up to 10 years earlier and later than dated. The program listed the effect on the correlation with the master series for the rings whose presence most lowered or raised the correlation coefficient. Rings that were more than 3.0 standard deviations wider or 4.5 standard deviations narrower than the mean of other series for that year were flagged. Along with visual inspection of the data and re-inspection of the cores, this information was used to identify possible dating errors. Missing rings were introduced by dividing the measurement of another ring, while false rings were removed by merging neighbouring rings. Such action was taken only when there was strong evidence to support it. In total, five series were adjusted for dating errors by adding or removing one ring. A new master series was created from the adjusted series for use in subsequent analyses.

Percentage growth change (%GC) due to harvesting was estimated from the relative growth performance of trees prior to harvest. Relative growth rates (RGR) of trees in pre-harvest years were calculated by dividing annual increments for each tree by the mean increment in control stands for that year. Expected growth in post-harvest years was then estimated by multiplying the mean increment in control stands by some function of RGR for each tree. Four such functions were evaluated. These were the 20 years (i.e., 1972–1991) pre-harvest mean, 10 years (1982–1991) mean, 5 years (1987–1991) mean, and last pre-harvest year (i.e., 1991) value. The function that most accurately estimated mean RGR after harvest (1992–2001) in control stands was then used to calculate %GC from expected growth E and observed growth O using Eq. 1:

$$\%GC = (O - E)/E \quad (1)$$

Variables were transformed to approximate a normal distribution using the square-root or logarithm where necessary. Because the nearest weather stations were around 100 km from the study site (Vincent and Gullett 1999), no attempt was made to relate diameter increments to climatic data.

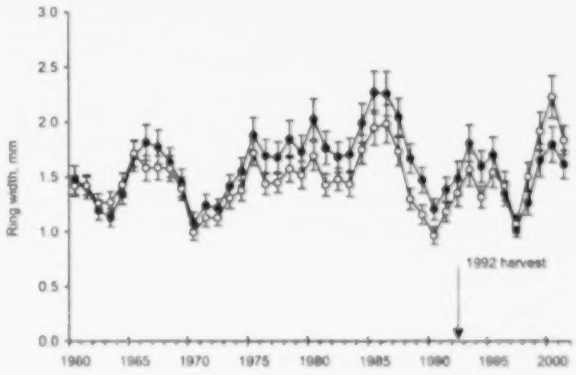

Fig. 1 Mean ring width, mm ± SE for cored white pines in harvested (*clear circles*) and control (*black circles*) stands from 1960 to 2001

Results

Pre-harvest total basal area of harvested stands was slightly lower than that of control stands, but there was no significant difference in white pine basal area (Table 1). Overall, basal area was made up of white pine (53%), eastern white cedar (10%), balsam fir (9%), white birch (8%), sugar maple (8%), red maple (6%), and white spruce (2%), with other species contributing less than 2% each. Approximately half the basal area of white pine had been harvested from harvested stands (Table 1). Mean white pine dbh was similar in harvested and control stands (Table 1). White pine diameter distribution was unimodal, with a minimum of 20.0 cm and a maximum of 104.0 cm (unpublished data).

Annual diameter increment series in harvested and control stands were highly correlated (r=0.79, P <0.0001). Harvested stand increments were on average 10.0% smaller than control stand increments between 1960 and 1995, were 13.5% greater between 1998 and 2001, and they were similar in 1996 and 1997 (Fig. 1). Differences between stand types prior to harvest were not statistically significant (repeated measures General Linear Model, P=0.3). Mean ring-width increments for all cored trees varied between 1.03 mm $year^{-1}$ ±0.06 SE in 1970 and 2.10 mm $year^{-1}$ ±0.13 SE in 1985, with a mean of 1.53 mm $year^{-1}$ ±0.04 SE for all years. Mean ring-width increments for 1960–2001 varied from 0.36 mm $year^{-1}$ ±0.04 SE for the slowest-growing tree to 3.8 mm $year^{-1}$ ±0.3 SE for the fastest-growing tree, with a mean ring-width increment of 1.54 mm $year^{-1}$ ±0.07 SE. The overall

Table 2 Performance of four functions of pre-harvest relative growth rate (*RGR*), defined as diameter increment in a control stand over mean growth increment for that year, in predicting mean post-harvest RGR. RGR in 1991 gave the most precise predictions (highest r^2) and was used to predict growth in harvested stands had harvesting not occurred

Function	Regression slope	r^2	P
RGR in 1991	0.95	0.74	<0.001
5 year mean (1987–1991)	0.96	0.64	<0.001
10 year mean (1982–1991)	0.97	0.67	<0.001
20 year mean (1972–1991)	0.97	0.64	<0.001

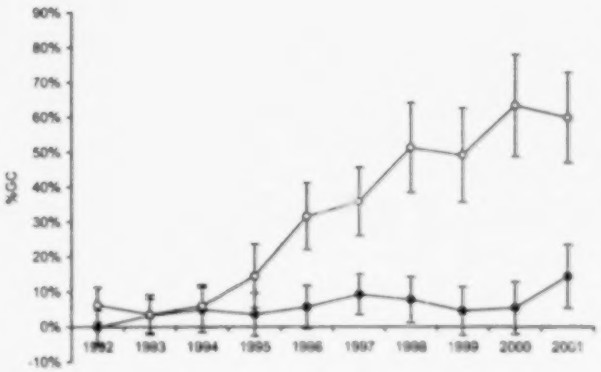

Fig. 2 Percentage growth change (%GC) ± SE in harvested (*clear circles*) and control (*black circles*) stands from 1992 to 2001

mean basal area increment was 0.003 m^2 $year^{-1}$ $tree^{-1}$ ±0.0002 SE.

Mean annual diameter increment between 1960 and 1991 was negatively correlated with total basal area estimate at the sample point (Pearson correlation controlling for stand treatment, r=–0.27, P=0.005) and with white pine basal area alone (Pearson correlation controlling for stand treatment, r=–0.24, P=0.011), but not with basal area of other species or with dbh (P>0.05). No attempt was made to reconstruct basal area for past years, since mortality and growth rates of other species were unknown.

Linear regression showed that RGR in 1991 most precisely predicted mean post-harvest RGR in control stands (i.e. highest r^2), while the 20 years pre-harvest average was most accurate (i.e. regression slope closest to unity). There was little difference among the four functions tested, indicating that RGR was stable over time (Table 2). To assess the methodology, growth rates were also predicted for control stands.

%GC in control stands did not differ significantly from 0 in any post-harvest year (t-test, P>0.1), with an overall mean of 5.9% between 1992 and 2001 (Fig. 2). In harvested stands, %GC began to increase in 1995 and was significantly different from 0 from 1996 onwards (t-test, P≤0.001). %GC reached a maximum of 63.3% ±14.6 SE in 2000. Harvested and control stand values differed significantly from 1998 onwards (t-test, P<0.01). Almost half (44%) of the trees in harvested stands had %GC greater than 100% for at least 1 year post-harvest, whereas only 4% of trees in control stands showed such a large increase in growth. From 1996 onwards there was a significant positive relationship between %GC and basal area of white pine removed from harvested stands (repeated measures GLM, P=0.011). The relationship was weak, however (r^2 varied from 0.038 in 1996 to 0.136 in 1999). %GC was not related to the proportion of basal area removed, the remaining basal area, total pre-harvest basal area, or dbh (repeated measures GLM, P>0.1).

Discussion

The data show that large, old white pines respond to removal of their peers by significant increases in diameter increments. This increase was first detectable at 3 years post-harvest, and increased through at least the first 8 years post-harvest. There was no indication of any negative growth response, or *thinning shock* (North et al. 1996). The percent growth change seen in harvested stands after harvesting, up to 60%, is larger than that (25%) used by Nowacki and Abrams (1997) to detect canopy release in ancient oaks. Almost half the trees in harvested stands showed the large responses (>100%) used by Lorimer and Frelich (1989) to detect release responses to natural disturbance.

High variability in growth responses in old white pines has been found in previous studies of unmanipulated stands. Abrams and Orwig (1996) provide individual chronologies for ca. 200 to 300-year-old white pines and other species in northwestern Pennsylvania, USA. The five oldest white pines, established around 1700, showed high initial growth, as expected, followed by low average growth (~1 mm $year^{-1}$) punctuated by growth spikes every 15–25 years for the first 100 years. A major release (sensu Lorimer and Frelich 1989) was seen even after 250 years of growth. Other white pines varied considerably in their growth patterns, some declining with age, others showing moderate or major releases after 200 years. Other species, including eastern hemlock [*Tsuga canadensis* (L.) Carr.] and beech (*Fagus grandifolia* Ehrh.) showed moderate releases (%GC of 50–100%) at ca. 250 years (Abrams and Orwig 1996). Canopy disturbance by wind storm was suggested as a possible cause for these releases. In contrast, a similar study in West Virginia, USA, by Abrams et al. (1995) found little evidence of growth release in trees more than 100 years old.

Patterns in tree-ring series are influenced by many endogenous and exogenous factors (Cook 1987), frustrating attempts to draw firm conclusions regarding past disturbance events. In this study, knowledge of the timing, amount, and type of disturbance, coupled with stand-level replication and availability of a control group (of the same species, geographical location, and similar stand age), removed much of the variability associated

with historical studies. In historical studies (e.g., Lorimer and Frelich 1989; Nowacki and Abrams 1997), no control groups are available for comparison, and growth releases must be indirectly detected by comparing within-tree growth in contiguous decades. This methodology has some limitations, including that assigned %GC values are influenced by releases several years in advance, and %GC may be underestimated because of averaging. For example, calculation of %GC using 5 years averaging of the data presented in this study would incorrectly suggest that harvested stands were released in 1991 (i.e., a year before harvest), and that the maximum %GC was ~30% (i.e. half the value calculated using direct comparisons of annual growth increments). Furthermore, the present study demonstrates that there is a substantial time-lag between disturbance and the peak growth response, therefore peak growth release responses cannot be used to date disturbance events unless the dynamics of the release response are known a priori.

Few prior studies have directly investigated the responses of large, old trees to partial stand harvest. North et al. (1996) found evidence of a thinning shock in 120 to 140-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] in Washington following a green tree retention cut. Over a 6 year period, post-harvest basal area increment was 15% lower in harvested stands than in unharvested controls. In contrast, Latham and Tappeiner (2002) detected a positive thinning response in 158 to 650-year-old Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and sugar pine (*Pinus lambertiana* Dougl.). Responses were greatest for ponderosa pine (around 60% greater after treatment than before), but smaller (~10–30%) for Douglas-fir and sugar pine. Youngblood (1991) found that thinning a 174-year-old white spruce stand in Alaska led to a 10% greater basal area increment over a 14 year period when compared with surrounding unthinned stands of similar age.

The growth increase detected in this study was thus higher than that observed in most other old-growth conifers examined to date, and for a large proportion of trees was similar to growth releases observed in white pine saplings (Stiell 1979). This result has implications for the widely-observed age-related decline in tree productivity (Ryan et al. 1997), particularly the idea that productivity declines are driven by age-related reductions in a tree's physiological capacity to respond to high resource levels. Although there have been no studies on white pine, other conifers often show a reduction in photosynthetic performance with age (Bond 2000), particularly when photosynthesis is expressed on a leaf mass basis (Thomas and Winner 2002). However, the link between these changes and growth dynamics remains unclear (cf. Weiner and Thomas 2001). In addition, age-related changes in the ability of conifer foliage to respond to increased light and other resources have received little attention (Cavender-Bares and Bazzaz 2000), but acclimation response rather than mean rates may be more directly related to the issue of age-related differences in thinning release responses.

>Diameter increment was highly variable through the study, but highly correlated among stands. This suggests external forcing by climatic factors. However, climatic responses tend to be muted in dense stands where competition and ecological interactions are intense (Fritts 1976), and previous studies have shown that white pine annual increment is poorly correlated with climatic factors (e.g., LeBreton and Beamish 2000). Such correlations are likely to be seen only in drought-prone sites such as ridges (Abrams et al. 2000) or areas where climatic variation is extreme (Vose and Swank 1994). Correlation between stands could also be explained by some internal mechanism operating among spatially separated trees. One possibility is synchronous fruiting that occurs in white pine every 3–7 years (Burns and Honkala 1990), which has been related to variation in ring size in other species (Koenig and Knops 1998). Unfortunately, cone-crop records are not available from the study area.

The response to thinning was not immediate, being delayed by around 4 years. Similar delayed responses have been found in other studies of conifers (Latham and Tappeiner 2002; Youngblood 1991). One possible explanation for this pattern is a gradual acclimation response. Sudden increases in irradiance or microclimatic changes may act to reduce potential growth until the tree has physiologically acclimated to the new resource regime. Since the acclimation response likely involves both changes in foliar characteristics and in allocation patterns (e.g., root allocation), one may anticipate that this process would require a period of years.

The present study has several implications for white pine management. White pine shelterwood treatments aim to promote seed production in remaining trees and to provide partial shade for regeneration. Further studies are required to determine whether the growth increases seen translate to increased seed production, though this is likely given that, proportionally, reproductive allocation is greater in larger, older trees (Weiner and Thomas 2001). To provide effective shade, residual trees must remain standing until regeneration has reached a height at which attack by white pine weevil is no longer a serious concern, a period of 20 years or more (Stiell 1985). Due to its great height and shallow rooting system, white pine is prone to wind throw (Foster 1988). Increased wind throw often follows thinning (e.g. Lohmander and Helles 1987), because trees in dense stands are not architecturally adapted to withstand wind-induced stresses (Petty and Swain 1985). Some evidence of increased wind throw was found in harvested stands in the Algoma forest (unpublished data). The increases in diameter growth seen in this study could reflect in part a change in allocation along the stem, increasing stem taper as an adaptation to withstand the force of the wind (Mitchell 2000). If this were the case, the observed increase in diameter growth would be valuable from both a silvicultural perspective, since residual trees would be more likely to remain standing and provide seeds and shade for regeneration, and from a conservation perspective, since old white pines are an important wildlife habitat feature (Naylor 1994).

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